The University of Chicago

THE AVIAN VISUAL SYSTEM

I. CEREBRAL FUNCTION OF THE DOMESTIC FOWL IN PATTERN VISION

A DISSERTATION SUBMITTED TO THE FACULTY OF THE DIVISION OF THE BIOLOGICAL SCIENCES IN CANDIDACY FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF PSYCHOLOGY
1934

By
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THE AVIAN VISUAL SYSTEM

I. CEREBRAL FUNCTION OF THE DOMESTIC FOWL IN PATTERN VISION[1]

JOHN D. LAYMAN

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I. INTRODUCTION

a. Avian vision compared to vision in other forms

The relative importance of vision and other senses in determining the behavior of different species of animals presents some interesting problems, both from the standpoint of evolution and from that of nervous organization. In some lower vertebrates as fish (Schaller, 1926) and reptiles (Casteel, 1911), detail vision seems well developed. It plays an important rôle in the life economy of these animals and is readily demonstrated under controlled experimental conditions. In birds, the primacy of vision is especially prominent. The apparent helplessness of most birds at night along with their dependence upon vision for feeding and for dexterously guiding them in their rapid flights bear witness to this fact.

In the macrosmic mammals, vision undergoes regression. Many of these are little handicapped when deprived of their eyes and in their normal activities they seem to make little use of vision (Tsang, 1934). In the rat (Lashley, 1912; Munn, 1929) and dog (Johnson, 1916c; Szymanski, 1918) it has been difficult to demonstrate even crude detail vision under controlled conditions. When a method is devised to force these animals to visual attention, they prove to have relatively good pattern vision

[1] The writer wishes to acknowledge his appreciation to Dr. K. S. Lashley for assistance in this project.

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(Lashley, 1930; Rizzolo, 1932), yet under ordinary conditions of life they seem dominated by other sense modes. It is only in the primates that vision acquires a predominance among the senses comparable to that in birds.

The reason for this dominance or suppression of vision in the higher vertebrates is not obvious from the structure of their eyes, nor from that of their central nervous system, but is to be sought in the physiological organization of the central visual pathways.

Besides throwing light on the problem of visual dominance, analysis of the visual function in birds offers a means of attack upon problems of binocular fusion. One of the most important cues to the perception of depth rests upon the fact of the binocular disparity existing between the two eyes in the perception of an object. In birds there is an arrangement in various species which fluctuates in some, from perhaps a complete overlapping of the visual fields, as in owls, to perhaps a complete separation in others, as in chickens. In some species there is no fovea; others have one and still others have two with various positions in the eye. There is complete decussation of the fibers in the optic nerve. Nevertheless, the rapid flight and accurate visual reaction to distance indicates a high degree of binocular integration carried out by a quite different structural organization from that of mammals.

b. Neural correlates of vision in birds and mammals

Anatomically the known nervous correlates of vision in birds and mammals differ tremendously. The point for clear detail vision is definitely known to be the fovea in primates. Yet according to Slonaker (1921) the domestic hen possesses no fovea, while on the other hand most birds possess one, and some two (Slonaker, 1897; Wood, 1917). In this later case the second or peripheral fovea is used in binocular vision.

In mammals, the fibers from the retina partially decussate in the optic chiasma, whereas in birds there is a complete crossing (Perlia, 1889). Further centrally in birds Perlia found a division into a medial and a lateral optic tract. These he correlated with

the nucleus of the medial optic root and the optic lobes respectively.

The central mechanism for detail vision in mammals is found in the occipital cortex. In primates and rodents, where the anatomic projection has been studied carefully, there is an accurate projection of the retina upon the surface of the cerebral cortex. Birds however, do not possess a highly developed cortex for a retinal projection although for them vision is one of the most important, if not the most important sense. Accordingly we see that there is great confusion as to the relation between visual dominance in these various animals and the central neural correlates. The question naturally arises concerning the nature of the central structure which accounts for the high development of vision in birds. Is the primitive cortex of the bird of primary importance for vision, or has evolution turned in another direction from the mammalian system and given increased powers to the optic lobes, hyperstriatum, or other striatal mass.

II. ANATOMICAL CONSIDERATIONS

a. Cortex

When the term cerebral cortex is used in avian literature, confusion at once arises. In mammals with a six layered cortex, the problem is simple. In birds however, even the best authorities differ as to what is designated by the word. Craigie (1929a) has a good summary of the diverging opinions on this point. Bumm in 1883, and Edinger, Wallenberg and Holmes in 1903 believed the whole striatum to be covered with cortex, while Kalischer in 1905 believed cortex was found only in the "wulst" region. (This "wulst" region in the chicken is a dorso-medial swelling in the anterior half of the hemispheres.) Later, Rose (1914) included only the area praepyriformis and septum pellucidum as cortical. Huber and Crosby (1929) recognize a hippocampal formation, entorrhinal and paraentorrhinal areas, and a dorsolateral surface area, as cortical. Of this latter striatal covering, they state that its inclusion as an area of cortex or not depends upon the definition of cortex. Craigie (1929b) dealing with the Australian Kiwi,

finds cortex over most of the dorsal and lateral striatum and in the ventral praepyriform area.

b. Striatum

Since many excellent descriptions of the avian striatal masses have been given in minute detail, only the major forebrain cell masses will be reviewed here. The recent excellent article by Huber and Crosby (1929) has been followed in terminology.

Figure 1 shows various levels of the bird forebrain. The letters indicate areas and correspond to the letters used by Rose in 1914 but the significance of these letters has been converted into the terminology of Huber and Crosby. The six different levels are indicated on the surface diagram of figure 2.

At the anterior pole, the whole forebrain with the exception of the basal olfactory nuclei is accessory hyperstriatum (*B*). At the level of the middle of the olfactory bulb two other large nuclei appear on the ventral surface and push the accessory hyperstriatum dorsally as seen in section 1 of figure 1. Traced farther posteriorly in sections 2, 3 and 4 the hyperstriatum accessorium is seen to diminish in size dorso-ventrally until, just before the anterior commissure it vanishes.

The first to appear of the two large ventral nuclei mentioned above is the hyperstriatum (*D*). This spreads out as seen in section 1 of figure 1 and is pushed upwards from its ventral position by the neostriatum. It fans out as in sections 2 and 3 and makes a gradual transition from this condition in the anterior region to that seen in sections 4 and 5 where it is pushed to the midline and eliminated.

The neostriatum (*G*) is the second of the two large basal nuclei previously mentioned, which take origin in the region of the olfactory bulbs. It continues posteriorly to the tip of the occipital pole as the largest mass of the forebrain (see sections 1 to 6, figure 1).

In sections 2, 3, 4 and 5 the neostriatum itself is seen to be pushed dorsally by four other nuclear masses of the forebrain. The first of these masses, the nucleus basalis (*R*) is seen only in the anterior regions (section 2). The second is the paleostriatum

(*H*) (sections 2 to 5) which appears just a few sections behind the nucleus basalis and continues posteriorly becoming smaller after the anterior commissure is reached and vanishing just caudal to the end of the hyperstriatum. A group of large cells (Sections 3 and 4) are found in the paleostriatum and called by Huber and Crosby paleostriatum primitivum (*J*). The other two masses are the ektostriatum (*S*) found in front of the anterior commis-

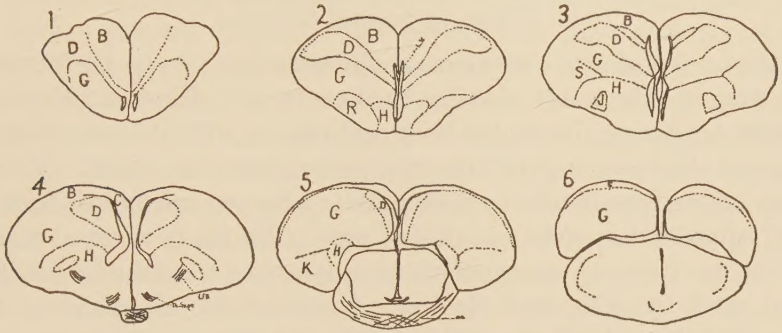


Fig. 1. Cross Sections of the Chicken Forebrain

For significance of lettering see text

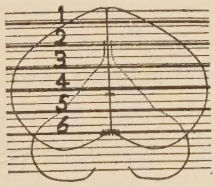


Fig. 2. Dorsal View of the Chicken Forebrain Showing the Levels of the Six Cross Sections of Figure 1

sure (section 3) and the archistriatum (*K*, section 5) found posterior to the anterior commissure. The basic thalamic and midbrain masses are best seen in sections 4, 5 and 6.

The homologues for all these structures with mammalian forms are not known. Paleostriatum is generally conceded to be homologous to the globus pallidus; the hyperstriatum inferius perhaps corresponds to the caudate and putamen; and the archistriatum is believed to be homologous to the nucleus amygdala of mammals.

Numerous fiber bundles pass out through the paleostriatum into the forebrain, but in a consideration of cortex only two bundles are of importance. The tractus septo-mesencephalicus connects the septum and adjacent cortex with the thalamus; and tractus thalamo-frontalis connects the thalamus with the anterior cortical areas.

III. HISTORICAL REVIEW

a. Vision in normal chickens

Many experiments on normal chickens have been performed showing the character of vision in these birds. Katz and Revesz (1909) by gluing rice to the floor and mixing with it loose wheat, trained chickens to avoid the rice and choose the wheat. They even trained the chicks to discriminate between triangles, circles, and squares that were cut out of peas. Doubt of course exists as to the value of an experiment employing a method such as that used by Katz and Revesz. However the experiments of Breed (1912), Bingham (1913, 1922) and Munn (1931) proved quite conclusively that chickens can discriminate between circles, squares, and triangles. These experimenters equated their figures both as to brightness values and size. Johnson in 1914, made a different attack on the question of avian vision. He determined the stimulus threshold for visible striae in chickens and found that these birds could make accurate discriminations even when the striae subtended an angle of 4 minutes 9 seconds. Two years later (1916a) this same experimenter showed that the ability of the common fowl to discriminate between different widths of striae was lost when the difference in width was reduced to a value between 33 and 40 per cent of the wider stripe. He further determined (1916b) that chickens could accurately discriminate between vertical and horizontal lines, but the threshold of discrimination was reached when the vertical-horizontal relationship was reduced to an angle of 25 to 40 degrees.

b. Electrical excitability of the avian forebrain

The divergence of opinion concerning the avian cortex is paralleled by contradictory evidence on the electrical excitability

of the bird brain. David Ferrier (1886) found a spot in the pigeon brain (medial and just behind the center of the brain in a rostrocaudal direction) that provoked an "intense contraction of the opposite pupil" when electrically stimulated. Boyce and Warrington (1898) also working on the pigeon, obtained the same response to faradic stimulation in a larger and more median area. In 1900, Kalischer localized by electric stimulation, areas for closure of the eyes and movements of the extremities, jaws, and limbs. Rogers (1922a), with perhaps an improved technique, obtained several points on the surface of the pigeon brain excitable to electric stimulation. Approximately the same area as that determined by Ferrier produced contraction of the opposite eye, while bilateral winking was produced by an area just lateral to the above named region. Contradictory evidence to the above has been obtained in the work of Popa and Popa (1933). These workers could obtain no response from the cerebral cortex with any intensity of either mechanical or electrical stimulation, even by plunging the electrodes deep into the hemispheres. They did find, however, localization of all motor activities in the midbrain. Like Rogers, they used pigeons. (In the chicken brain by using faradic stimulation, I have localized a motor area for contraction of the pupil of the opposite eye, corresponding approximately in location to the area indicated by Ferrier and Rogers for the pigeon.)

c. Extirpation work on the bird forebrain

In the literature of the past describing the anatomy of the bird forebrain, or reporting experiments performed thereon, two principle faults appear. In the first place, there has been no consistency in nomenclature of structures. Moreover, some workers have applied terms to one structure which have been used by other workers to indicate different structures. Secondly, where cerebral ablations have been performed, it has not been the general rule to report necropsies.

Quite uniformly, experimenters have reported that cerebral ablations in birds produce visual disturbances. Their operations have been performed on all parts of the forebrain and as a result,

all parts of this mass have been looked upon as producing visual anomalies. Whether the defect in the various cases resulted from the brain injury in a specific region, or resulted because of a lowered mentality of the experimental subjects is not considered.

Extirpation procedures in birds have been performed for over a century. Rolando in 1823, by using a spatula removed cerebral tissue in the parietal region and produced inaccuracy in seizing grain. In 1842, Flourens produced unilateral and bilateral cerebral ablations in pigeons and hens. In the former type of destructions he reported blindness in the opposite eye whereas total blindness resulted from bilateral decerebration. On the other hand, Longet (1842) removed both hemispheres in pigeons and stated that these animals still flew. Whether they could see or whether they struck obstacles is not mentioned. Schrader's work in 1889 on decerebrate birds showed visual deficiencies which were confirmed by Boyce and Warrington in 1898. The latter found that interference with one hemisphere produced a "deficiency of vision in the opposite eye," and that "This result occurs after removal of the anterior or posterior portion of the cerebral hemisphere." Edinger (1895), from anatomical considerations, believed that the occipital pole was visual, and Kalischer (1900) from experimental work, arrived at the same conclusion. Treves and Aggozzatti (1901) worked on bilaterally decerebrated pigeons. They reported that one bird learned to fly back to its perch from new positions in the room, thus indicating that it could still see. In 1918, Martin and Rich working on white leghorn chickens found that with just the upper pallial layers destroyed, feeding was normal, indicating that vision was still intact. Shaklee (1921), moved by the work of Martin and Rich began to work on decerebrate pigeons. Although this experimenter made no visual tests, the results indicate the absence of vision. A great amount of work on decerebrate pigeons has been done by Rogers (1922b). When he obtained unilateral decerebration (checked by histological work) he, like many others, obtained visual defects in the opposite eye. In quite recent years, Gemelli and Pastori (1930) after first training chickens to discriminate colors, decorticated them bilaterally. They found

that the animals could be retrained to discriminate colors, showing that this form of vision was still functional. Moreover the fact that these animals discriminated various grains, points to the retention of a crude detail vision. Although many other workers have performed extirpation experiments on birds, their results do not indicate the presence or absence of vision after the lesions had been made.

A brief résumé of previous work thus indicates that with one exception, experimenters have been able to obtain motor responses by electrical stimulation of the forebrain; but agreement as to the locus of stimulable areas and results obtained, is by no means perfect. Other experimenters by using extirpation methods quite unanimously find visual disturbances resulting from cerebral ablations. The tests for vision in these cases however have all been crude and the failure on the part of the animal to react to visual stimuli cannot be taken as proof of blindness.

IV. PROGRAM OF STUDY

a. Statement of problem

Before we can attack such problems as those of ocular dominance or binocular fusion, for which the study of birds promises to be of especial value, we must determine the rôle of the various optic structures in detail vision. We have therefore undertaken an analysis of the effects of destruction of various central nervous structures upon the chicken's ability to differentiate visual patterns. The present study is concerned with the cerebral hemispheres, and principally with the cortex. The experiment was outlined to answer the following questions.

1. Is there an area of the cortex of the chicken essential for pattern vision, such as Lashley (1931) has found to be the case in the rat?

2. If there is no specific visual cortical area, what part if any, does the cortex play in vision?

3. Is any area of the striatal mass more influential in vision than the rest of the mass?

The previous discussion of avian cortex means that in any

attempt to destroy this pallial covering we would of necessity either (*a*) limit the lesions to agree with one anatomist's conception of what is cortex, (*b*) attempt to destroy all areas recognized by all writers. The latter has been attempted in this work. So conceived, the cortex includes the area of the septum and the entire covering of the occipital pole. Anteriorly, where the ventricles are restricted to the midline, the superficial dorsolateral surface areas together with the areas between the upper tips of the ventricles and between their anterior continuation would be included in such an attempt.

b. Apparatus

The discrimination box has proved to be one of the most satisfactory means for the study of vision in animals. In experiments using this box, the stimulus cards have marked the ends of the discrimination alleyways and the subjects, having arrived at this point have had to turn away from the stimulus card to obtain their reward. The work of Bingham (1922) and Munn (1931) on chickens, indicates that several hundred trials would have been required for the high criterion which I used in this experiment. To work with large groups of operated animals therefore, some procedure making possible more rapid learning was desired.

In the method employed, a modified Yerkes' apparatus shown in figure 3 was used.[2] The essential difference between this box and that used by Cole (1911) and Breed (1912), was that in this case the figures to be discriminated consisted in holes cut in a sheet of white cardboard (*E*). In this manner the animal went directly to the figures to be discriminated and by placing its head and neck through the correct hole, obtained food. The food behind the incorrect figure was usually covered, but when it was not, an appropriate shock was administered which easily prevented the animal from obtaining grain. As seen from figure 3, the length of the cardboard was sufficient to allow it to be slipped back and forth in its position. In this manner, changes in the

[2] The writer is indebted to Mr. Neil Van Steenberg for drawing the apparatus shown in figure 3.

position of the positive stimulus were made. The food chamber was painted black. Accordingly from the front of the apparatus, the figures appeared as dark holes cut in white cardboard.

c. *Procedure*

In training the birds, a preliminary period of three days preceded the actual experimentation. During this period, the

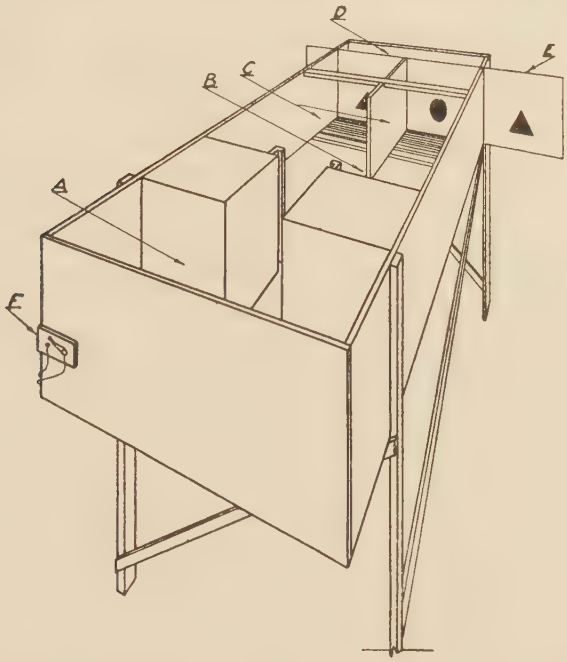


FIG. 3. DIAGRAM OF THE APPARATUS USED IN THIS EXPERIMENT

A, starting box; *B*, discrimination chamber; *C*, grid compartments; *D*, food chambers; *E*, discrimination card; *F*, switch.

animals were allowed to remain in the box for two hours daily to become acquainted with the apparatus. Both food boxes remained uncovered. By being frequently removed from before the food boxes on the first day and replaced within the starting box, the hungry birds readily learned to hasten to the food. On the second and third of these preliminary days, a three inch white

cardboard was placed before the food boxes in the slit, which during training held the discrimination card. The birds had to reach over this obstacle to obtain their food during this period.

The birds were fed once daily, directly after training. Only ten trials were run each day, although the animals were still hungry when training ceased. Morning proved to be the most desirable time to train.

The chickens were individually removed from their cages and placed within the starting box of the apparatus in the same manner, location and direction, to avoid giving them a clue as to the location of the correct choice box. When they had finished a trial, they were removed from the box with the left hand, the experimenter standing to the right of the apparatus. This made for uniformity in handling the birds with the left hand while at the same time the card could be shifted and the position of the cover to the food boxes changed with the right hand. To avoid possible cues, the card was occasionally shifted back and forth several times, before the bird was replaced in the starting box.

Most chickens rapidly learned to reach through the holes in the card. As reward for a correct choice they were allowed to secure a few grains of scratch feed from the food box. No food was available from behind the negative form, for as stated above a cover was placed over this box. Nevertheless, very often on a wrong choice the chickens pecked vigorously at the cover which was preventing them from obtaining food.

Ordinarily a wire cover was placed over the entire apparatus during the first few days of training. This was unnecessary in later trials unless a severe shock was administered, in which case the chickens flew out of the box. In the initial part of this experiment, punishment was administered for a fraction of a second on every wrong choice, but later was reduced to one or two shocks for every 50 trials.

The learning criterion was set at 20 consecutive correct responses or 29 correct responses out of 30 attempts. Animals were considered to have failed when they had made 1000 trials and in this time had not reached the criterion of success. Some animals which in reality did give evidence of learning by making as high

as 88 per cent correct in 60 consecutive runs were considered failures because of this high criterion. These will be considered separately in the results. A few other animals learned the problem but were considerably retarded and fell above the three sigma (620 trials) range of the controls. In later discussions these will be considered as retarded cases.

When learning had occurred, the animals ran rapidly to the positive stimulus. Several checks were then used to ascertain whether they were reacting to cues arising in connection with the discrimination card or had actually learned the problem. Thus the following were used: (1) new stimulus cards were made and used, for cards long in use always showed marks of wear; (2) the cover was removed from the food box behind the wrong stimulus; (3) occasionally the food box behind the correct figure was covered and that behind the incorrect form left open (this caused the birds to pace back and forth between the discrimination chamber and the covered food box); (4) the card was at times, shifted quickly while the animal was hastening over the discrimination chamber (a shift in the animal's direction was interpreted in this case to indicate discrimination on the basis of vision); (5) lastly, some birds after learning required coaxing to enter either alleyway when the discrimination card was removed or a narrow three inch cardboard substituted in its place.

Several other checks were made during training to avoid the possibility that the animals might pick up a cue. Thus I sometimes turned my back toward the apparatus and observed the animals with a mirror. Extraneous noises were minimized as much as possible or were at least constant in position. The brightness of the two alleyways was as nearly constant as possible since the apparatus was placed directly before and in the center of a large window. Lastly, other experimenters have trained the animals after learning had occurred without any effect upon the animals' ability to discriminate.

d. Animals

The chickens were all young pullets approximately nine to twelve weeks old when purchased. White leghorn pullets were

preferred because of their activity, but during the winter months these could not be obtained and nineteen barred rocks were substituted. Examinations of both the objective records and the lesions showed no difference between these two groups.

The food used as incentive was a combination of yellow cracked corn, wheat, barley and milo maize. Besides this ration of hard food obtained as a reward, growing mash mixed with a little water was given just after training. At first, cod liver oil was mixed with the mash, but later it was given directly with an eye dropper three times a week. Lettuce and meat were also given when available.

e. Operative technique

In attempting to localize the area for pattern vision in the chicken cortex, I tried to make a survey of the surface of the whole forebrain. The method used consisted in destroying various areas of brain tissue under consideration. The subject was etherized, feathers clipped, scalp longitudinally slit, skull trephined, and tissue destroyed with an electric cautery. The whole procedure was performed under aseptic conditions. Both hemispheres were operated upon simultaneously. An attempt was made to produce symmetrical, bilateral lesions. The scalp was closed by interrupted sutures and a celloidin bandage applied to prevent scratching of the wound. In most cases, after two weeks the birds were entirely recovered. They were then started in the discrimination apparatus. A few, because of severe lesions had not recovered after several weeks, and five were fed by hand for a considerably longer period than the time required by the average operative case to recover and learn the problem.

f. Histological procedure

Having learned or failed to discriminate, the animals were brought to necropsy. Their brains were fixed and hardened in 95 per cent alcohol, imbedded in celloidin and sectioned at 50 μ. Every fifth section was saved. In this manner four sections were

obtained per millimeter. A series of sections was cut covering the entire area of lesion in both hemispheres. About half the brains were stained in iron hematoxylin, the other half in thionin. The sections showing lesions were drawn under camera lucida and the extent of lesion determined under high power and marked on the drawings. From these drawings a composite picture of the lesion was obtained showing the actual extent of destruction on the surface of the brain (plates I to V).

The primary purpose of this project was to investigate cortical activity in relation to pattern vision. Depth of lesion was thus very important, because the cortex is superficial except in the septum where some of it is far removed from the dorsal surface. In the reconstructed lesions shown in plates I to V, I have attempted to show depth by using three different markings: (*a*) stippling, (*b*) black parallel lines, (*c*) total black. Lesions were considered shallow when they did not involve more than the cortex. In the septum where the cortex is thick, lesions were considered shallow when they did not extend to a depth greater than six cells. These lesions are represented by stippling. Lesions that destroyed the forebrain material below the cortex but in which the lesions did not reach to a depth of one half the forebrain are shown in parallel black lines. Such lesions destroyed the upper cortical layers and may have pierced almost to the paleostriatum. The deepest lesions are indicated by the total black areas and represent regions in which the destruction or degenerative changes are found to a depth of at least one half the forebrain. One further marking is found in a few sections. Occasionally degenerative changes were found to have undercut surface areas which showed no lesion. These were usually small areas and have been indicated in the diagrams of plates I to V by small circles. Most dorsal surface lesions show only small destruction when viewed laterally. However when deep dorsal lesions occur and are viewed from the side, the lateral surface appears intact but undercut. This accounts for the large areas of circles in some reconstructions.

V. EXPERIMENTAL DATA

a. Learning by normal birds

Ten unoperated white leghorn pullets learned the problem. With but one exception the records for these animals all fell below 320 trials and 100 errors. As seen in table 1, the range is from 119 to 498 trials with an average of 256.9. The errors range from 49 to 155 with an average of 82.8.

Six of these animals were tested for retention two weeks after meeting the criterion. With only one exception, retention was perfect.

TABLE 1

Summary of training records of normal animals

CHICKEN	TRIALS	ERRORS
1	498	155
2	300	88
3	320	97
4	262	90
5	242	83
6	140	50
7	264	87
8	272	73
9	119	49
10	152	56

b. Learning by operated birds

Out of 50 operated birds only 6 failed to reach the high criterion of 20 consecutive errorless runs, or one error in 30 trials. The records of these animals are given in table 2. Column S shows the total area of destruction (lesions in both hemispheres summed for the single figure). Column DS shows the total area of lesion weighted for depth. Trials and errors are also presented.

The surface reconstructions of the cerebral lesions in these animals, together with typical cross sections are found in plates I to V. The arrangement of cases in table 2 and in plates I to V has been made on the basis of trials. This has placed all the failing cases together. An arrangement based on errors would

TABLE 2

Summary of training records of animals with forebrain lesions

S = total surface area of lesion. DS = total area of lesion weighted for depth. Tr. = trials. Er. = errors.

NUMBER	S	DS	TR.	ER.	COMMENTS
1	28	30	60	16	
2	79	106	93	35	
3	43	63	135	42	
4	24	24	141	39	
5	35	66	141	63	
6	34	39	158	57	
7	51	78	163	60	
8	85	194	181	75	
9	54	85	185	36	
10	61	93	187	66	
11	35	55	188	56	
12	61	101	205	85	
13	30	99	206	109	
14	39	49	212	82	
15	80	84	221	73	
16	52	87	234	90	
17	45	85	234	91	
18	79	124	252	73	
19	33	52	252	85	
20	47	73	256	61	
21	66	91	276	109	
22	35	69	312	122	
23	89	143	316	112	
24	80	162	316	147	
25	41	53	321	78	
26	83	122	322	109	
27	36	62	353	101	Made 90 per cent correct by 80th trial
28	27	27	357	100	Made 90 per cent correct by 200th trial
29	46	102	364	118	
30	54	70	428	203	
31	56	73	437	188	
32	56	71	462	219	
33	97	237	480	171	Made 90 per cent correct by 240th trial
34	59	75	507	211	Animal was very lazy
35	60	123	526	182	Made 93 per cent correct at 330 trials
36	78	181	542	212	Had leg weakness
37	52	84	576	207	
38	31	38	578	287	Had roup at one time
39	50	89	631	248	
40	42	49	637	271	Frightened at trial 350
41	129	321	655	352	
42	82	179	665	299	
43	132	306	711	375	

TABLE 2—*Concluded*

NUMBER	S	DS	TR.	ER.	COMMENTS
44	102	231	727	220	
45	39	79	1,000	360	Made 88 per cent correct, trials 490–550
46	74	126	1,000	388	Made 84 per cent correct, trials 620–680
47	122	268	1,000	462	Made 80 per cent correct, trials 510–540
48	52	85	1,000	500	Animal frightened and erratic
49	86	180	1,000	598	Animal listless and anemic
50	50	88	1,000	510	No indication of learning

have only slightly altered the arrangement for there was a rank order correlation of .943 between trials and errors.

Variation in learning is shown in figure 4, where the normal and operated animals are compared as to trials required in learning

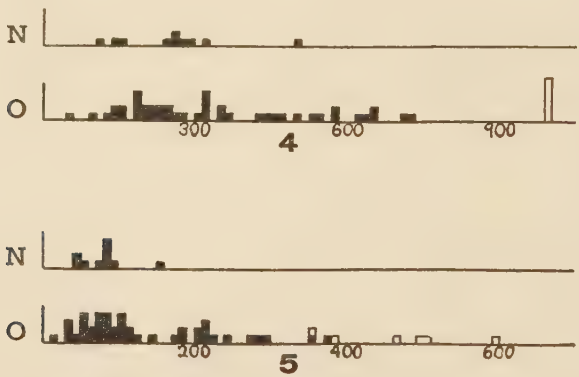


FIG. 4. DISTRIBUTION OF NORMAL (*N*) AND OPERATED (*O*) ANIMALS AS TO TRIALS REQUIRED

Black areas indicate animals that learned; unfilled areas those that failed

FIG. 5. DISTRIBUTION OF NORMAL (*N*) AND OPERATED (*O*) ANIMALS AS TO ERRORS MADE

Black areas indicate animals that learned; unfilled areas those that failed

the discrimination. The animals which failed are indicated on this chart with unfilled squares whereas total black squares indicate those which learned. Figure 5 is a comparison of operated and unoperated chickens with respect to errors made, and here again unsuccessful cases are represented by open white squares.

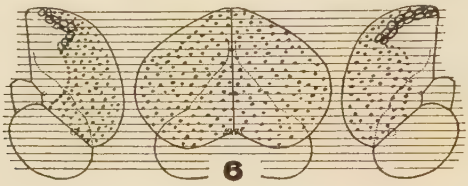
These histograms show that the normal animals were superior to the operated animals both as to trials required and errors made.

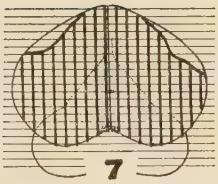
1. Animals learning within the lower 75 per cent range of normal animals

A cursory glance at plates I to V indicates that all the dorsal and most of the lateral surface regions have been destroyed at least superficially. A composite diagram showing the entire area of destruction in those animals which learned within the range of the lower 75 per cent of normal chickens (that is up to 339 trials) is seen in figure 6. With the exception of a small bit of tissue on the lateral anterior sides, the entire dorsal surface has been explored in these animals. The first 26 animals of table 2 are included in this group. Since these animals learned as though they were normal, the characteristics of their cerebral ablations are important. Animal number 8 of this group learned in 181 trials, well below the average for unoperated chickens, and yet the lesion shows most of the posterior cortex destroyed, together with very deep accompanying destructions. Chicken number 13, with lesion destroying much of the anterior cortex not destroyed in the case of number 8 is also included within this group. Thus in two animals, most of the posterior and central anterior cortex is destroyed together with the underlying striatum, with little or no effect on vision. By inclusion of the other 24 cases of this group, the total surface area destroyed is increased to the proportions indicated in figure 6. Figures 7 and 8 are composite drawings of the medium deep and deep lesions respectively in this group of operated, but normally behaving animals. From these three figures (6, 7, 8) two facts stand out prominently. In the first place, the total extent of surface area explored is almost as great as the surface area of the brain; and in the second place, the deepest lesions occurring in this group of 26 animals are largely confined to the posterior half of the brain. These results demonstrate that the capacity for detail vision may survive the destruction of every part of the cortex of the bird, even when the lesions are of considerable magnitude. They do not substantiate the opinion that the occipital pole is visual.

2. Animals much retarded in learning

There are 12 animals, number 27 to 38, which learned the problem, but in point of behavior records they fell above the 75th percentile (339 trials) and below the three sigma mark (620 trials) of the normal animals. This is a range not beyond the normal probability of occurrence. However, when it is remembered that only 26 animals occupied the lower 75 per cent of the distribution, there is suggestion of a retardation other than chance. On observing the reconstructed lesions (plates III and IV) of these





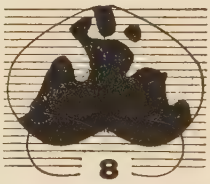


Fig. 6. Combined Surface Lesion of Operated Animals Learning Within the Range of the Lower 75 Per Cent of Normal Cases

Fig. 7. Combined Medium Deep Lesions of Operated Animals Learning Within the Range of the Lower 75 Per Cent of Normal Animals

Fig. 8. Combined Deep Lesion of Operated Animals Learning Within the Range of the Lower 75 Per Cent of Normal Animals

12 animals, one sees that they scatter over the whole surface of the diagrams, and have nothing more in common than those which learned more rapidly. The only explanation which I can offer for the fact that so many cases fall in this range is that the lesions produced a mild dementia which in turn reflected on the behavior records.

Above the three sigma mark of normal animals, there are six other chickens which learned (numbers 39 to 44). The main

characteristics of the lesions in these subjects are that they are relatively large and posterior. I believe that size, rather than locus of injury, explains the retardation of these animals since there is reason to suppose that more severe dementia would result from larger than from smaller lesions.

3. Cases failing within the training period

We saw previously that practically all surface areas were destroyed without any noticeable effect upon vision. There were however, six animals (45, 46, 47, 48, 49, 50) which did not reach the criterion of success in 1000 trials. Two of these animals gave evidence of discrimination: chicken 45, which eventually ran 88 per cent correct in 60 consecutive trials, and chicken 46, which made 84 per cent correct for the same number of successive attempts. Of the other four animals, number 47 reached an efficiency of 80 per cent correct for 30 consecutive runs. Later, this animal became frightened and failed. Animal 48 became frightened quite early in training and never overcame her fear. Case 49 was in poor physical condition most of the time. The remaining animal, number 50, alone never gave any sign of learning the problem. She was not ill at any time.

In view of the above considerations we could dismiss the first five failing cases as either discriminating, or failing, due to poor health or fright, and conclude that only one animal really failed. However, as this procedure would be radical we shall consider these cases in more detail.

If for a moment one refers to figure 5 where the error records of the birds are shown, it is readily seen that two animals (45, 46) had error records comparable to the worst of the cases which satisfied the criterion of success. This indicates again that these two animals could discriminate. A third doubtful case as mentioned above is animal 47. As the error record of this animal was fairly high, I shall consider it together with animals 48, 49 and 50 as failures.

A composite diagram of the lesions of these four animals is seen in figure 9. This figure shows two main facts. In the first

place, the posterior and postero-lateral areas are uninjured. This again is in disagreement with the statements in the literature that the posterior pole in birds is visual. In the second place, it is seen that with the exception of the occipital pole and the lateral occipital areas, the regions explored in the failing cases are identical with the regions explored in the successful animals.

Analyzing these four cases in search of some similar cause for their failure, the depth of lesion must be considered. Figure 10

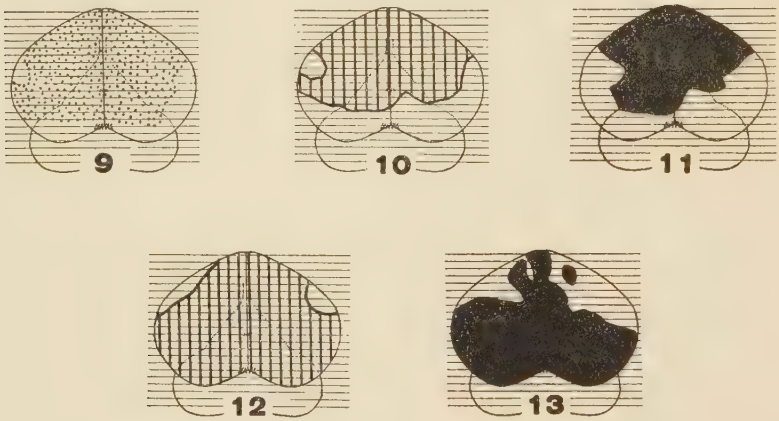


Fig. 9. Composite Diagram Showing Total Extent of Surface Explored in Animals Which Failed

Fig. 10. Combined Medium Deep Lesion of Animals Which Failed

Fig. 11. Combined Deep Lesions of Animals Which Failed

Fig. 12. Combined Medium Deep Lesion of Animals Which Learned

Fig. 13. Combined Deep Lesion of Animals Which Learned

shows a composite lesion of medium depth while the composite deep lesions are represented in figure 11. For comparative purposes figures 12 and 13 are diagrams of the lesions of all successful animals and represent the combined medium and deep lesions of these cases. It can be readily seen that there is much overlapping. In the medium type of lesion there is a little antero-lateral tissue destroyed in the cases that failed to reach the criterion (fig. 10) that is not destroyed in the cases that were successful (fig. 12). However, this area is found in only one of the failures

(47). The same follows for figures 11 and 13. In the case of these deep lesions, much more anterior tissue is destroyed in the failures (fig. 11) than in any of the successful animals (fig. 13). Here again it was the same animal (47) which showed a unique lesion that was not paralleled by a similar lesion in any of the successful cases. In consideration of the training record of this animal, the probability that the unique deep regions destroyed in this case are the essential areas for pattern vision while admissible, is remote.

A composite lesion of areas common to all the four failing cases is found in figure 14. It can hardly be possible that these two areas are the essential regions for pattern discrimination per se, for after a consideration of animals 2, 10, 13, 35 and 41 we see

Fig. 14. Common Area Destroyed in Cases Which Failed

that these areas have been destroyed in cases which learned readily.

In view of the above considerations, it is quite apparent that there was no single area of the brain destroyed in these unsuccessful cases which could have caused failure. Only animal 47 had an area unique to itself and as stated before, this bird gave some evidence for discrimination.

4. Animals learning with striatal lesions

Thus far in this paper, little consideration has been given to particular striatal nuclei, except to group them into the deep or medium category. I shall consider them briefly at this point. An attempt has been made in figure 15 to project roughly some of the larger forebrain nuclei onto the dorsal surface. The location of these projected masses will vary with the points chosen for

projection. Furthermore, depth of structure cannot be shown. Thus the posterior tip of the accessory hyperstriatum is very thin, but in the anterior areas it extends to the base of the brain. The six levels indicated in figure 2 are also indicated on figure 15 for orientation. By superimposing the diagrams of plates I to V upon figure 15, a rough idea can be obtained of the subcortical structures involved in the lesions.

Two animals (41, 43) with all the striatal masses posterior to the anterior commissure destroyed, learned the problem. The archistriatum and half of both the paleostriatum and neostriatum were destroyed in these animals. The lesions in cases 13, 19 and 22 are medially located and have destroyed most of the accessory hyperstriatum. Nevertheless, vision functioned normally in

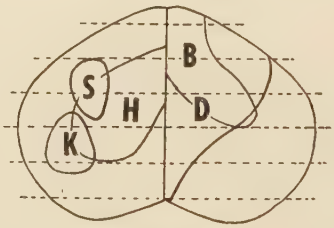


Fig. 15. Projection of Some of the Main Striatal Nuclei onto the Dorsal Surface of the Forebrain

For significance of lettering see figure 1

these animals. The remainder of the forebrain masses, the hyperstriatum, the anterior parts of both the paleostriatum and neostriatum were invaded in other cases, without noticeable effect on the ability to form the visual discrimination habit. The lesions in each case were small and no combined lesion would show all of these areas destroyed. These anterior nuclei were all invaded, and for the most part destroyed in one case (47), and this animal did not learn. Accordingly, there are subcortical areas in the anterior region that were not abolished in successful animals, that were in one animal that failed. The inference seems to be that whereas huge subcortical lesions in the posterior pole do not abolish vision, huge subcortical lesions in the anterior areas do.

5. Extent of lesion in relation to retardation

According to the results, no distinct area such as we find in mammals seems to be critical to pattern vision in chickens. Some other system must have developed in birds which serves the same purpose in them, that the visual area does in mammals. In search for such a system in the forebrain of birds, I have followed up two possibilities. The first was that vision is correlated with mass of cortex in the bird.

To determine this, the planimeter was used to measure the total area of the lesions and these were then correlated by the rank order method with trials required to master the problem. If the formation of the visual habit was dependent upon mass of cortex, correlating total surface area destroyed in each hemisphere with behavior records should have given a significant figure. The results were low, a correlation of only $+ .22 \pm .09$ was found.

There was another possibility in connection with mass effect. Formation of the visual habit might be correlated with mass of the whole forebrain. To determine this, two other planimeter readings were taken; one measured the areas for the medium deep lesions and the other those for the deep destructions. The former of these two was given double weight and the area for deep lesions was given a triple weighting. These weightings together with the planimeter readings for the total surface areas were then summed and this sum was correlated in the same manner as above with trials. The result in this case was $+.39 \pm .08$. This figure is low, yet it is higher than the correlation between surface area destroyed and trials.

There is an indication in these results which shows that large surface lesions tend to be more detrimental to the visual problem than small lesions. There is a stronger tendency which indicates that the formation of the visual habit is dependent upon total mass of forebrain tissue as a whole. However, as previously mentioned, destruction of cerebral tissue may produce a dementia for learning which prevents formation of a visual habit, although vision may remain. Again, cerebral ablations may produce inertia in the animals and thus favor failure.

6. The possibility of a dual control

Another possibility for a central visual mechanism is that the bird might have some sort of dual control for vision in the forebrain, and that to destroy vision, both these controlling areas must be destroyed. In figure 14 we saw that there were two areas common to all failing cases. Parts of these, rostral to the anterior commissure are bilaterally symmetrical with two common areas as represented in figure 16. If these areas per se, were the cerebral visual controlling mechanism, then in all animals with these areas destroyed detail vision should be wanting. Yet in connection with figure 14 we found animals 2, 10, 13, 35 and 41 that had lesions in these regions and detail vision still existed.

There is a further possibility, inasmuch as these common areas

Fig. 16. Bilaterally Symmetrical Areas Common to All Animals Which Failed

together may represent only one part of a vicariously functioning system. The failures not only had these common areas ablated but they also showed some, if not considerable destruction of other anterior areas. It may be possible then, that a certain amount of cerebral mass with indefinite locus rostral to the anterior commissure plus the areas shown in figure 16, which when destroyed will produce a deficiency of vision as shown by failure in pattern vision tests. More cases are needed to settle this possibility.

VI. DISCUSSION

The training records for both trials and errors in the operated animals showed considerably more dispersion than those of the normal animals. The lesions were scattered over the whole sur-

face of the forebrain, but there was no consistency found between the loci of lesions and retardation in learning. This may mean that lesions in any region merely accentuate the normal variability existing among the animals.

The existence of a cortical retina, or even of a combination of cortical areas which when destroyed, would abolish detail vision, was not found. This pushes the search for a visual correlating center down into the forebrain nuclei, if not into the diencephalon. Certainly the posterior striatal nuclei are uninfluential in the perception of detail vision. The anterior striatal nuclei were all separately invaded in various animals which learned, but they were all invaded together in one animal which failed to reach the criterion. This suggests that destroyed together they would prevent the formation of visual pattern habits, whereas when individually destroyed they would not.

One writer (Elliot Smith, 1919) considers the accessory hyperstriatum as the primordium of the neopallium of mammals. That this neopallial area in its entirety may be the essential area for pattern vision is indicated by the results obtained on animal 47. As stated above, this animal with all this area destroyed failed, whereas those animals with just invasion into the area, learned.

We know that brain tumors, hydrocephalism, cerebral wounds and the like, produce a dementia in human beings. We also know that by certain destructions in the human brain, intelligence may be lowered and vision remain intact. The same may be true of chickens. Capacity to learn may have been effected without detriment to vision.

Phylogenetically, we find an increasing neural organization from lower to higher animals. In mammals, a highly developed visual system in the forebrain is found. This is not so in birds, even though both phylla have branched from reptiles. One hypothesis which might explain this lack of a visual cortex is the belief that birds have developed from a different reptilian branch than have mammals and as a result the disposing tendencies to development may have differed and a highly developed cortex result on the one hand, whereas on the other it would not have

developed or would have developed only slightly. This idea however is not supported by the evidence as found by Craigie (1929b) that in the more primitive birds such as Apteryx, more cortex is found than in the more developed birds. This suggests that evolution in avian forms has followed a course different from that in mammals and that after a certain complexity of cortex had been developed, instead of developing more complexity it has actually degenerated in importance and that structures have assumed importance in birds which in mammals are less influential or non existing. The hyperstriatum complex may be one of these more important areas in birds. Another area, and one which we believe is connected with vision in mammals, is the mid brain. It is certainly a region of relatively high development as judged from external size. Yet what part the mid brain or optic lobes, play in avian vision is a question yet to be settled.

VII. SUMMARY

Cerebral injuries were performed on 50 chickens, after which they were trained on a modified Yerkes-Watson discrimination apparatus in a test for evidence of pattern vision.

1. All regions of the cortex were destroyed. No area of this superficial covering was found essential to the formation of the discrimination of visual patterns.

2. Contrary to the results of workers on mammalian forms, it was found that the cortex is not essential to vision. However, if the lesions were sufficiently large, a defect in learning the visual problem was apparent, and feeding reactions were slower. I believe that this is not so much a visual defect as it is a lowering of the general intelligence of the subject.

3. Both large (superficial) and deep lesions in any region were more deleterious to learning than smaller lesions in any region. This points to some sort of a mass effect of cerebral tissue in the formation of this visual habit. Posterior lesions showed this tendency quite uniformly but there were several discrepancies in the anterior regions. The correlation between superficial area destroyed and trials was $+.22 \pm .09$. The correlation between depth of lesion or volume of tissue destroyed, as determined

by a purely arbitrary method of weightings, and trials was $+.39 \pm .08$.

4. Six out of fifty cases failed to reach the criterion of success. Two of these gave evidence of discrimination. The lesions of the remaining four failures were located mainly in front of the anterior commissure, but as many successful cases showed lesions in these same regions, destruction of the anterior region per se, did not cause failure to learn.

5. An area common to all the failing cases was found. As there were many cases which learned with lesions in this same region, destruction of the area itsef was not the cause of failure in these four cases.

6. Some basal nucleus or combination of basal nuclei in front of the anterior commissure may influence the interpretation of visual signs. Only by multiplication of cases can this be determined.

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EXPLANATION OF PLATES

The reconstructed lesions of the 50 operated animals are found in plates I to V, which show a dorsal and a lateral view of each brain. To the right of each reconstructed case are typical cross sections through the center of the lesion. The numbers on the dorsal views refer to the number of the animal. Four kinds of markings have been used: (1) solid black, representing either areas of deep lesions on the surface diagrams, or degenerated areas in the cross sections; (2) parallel vertical lines, representing the medium deep lesions; (3) stippling, representing surface lesions and; (4) small circles, representing undercut areas.

PLATE I

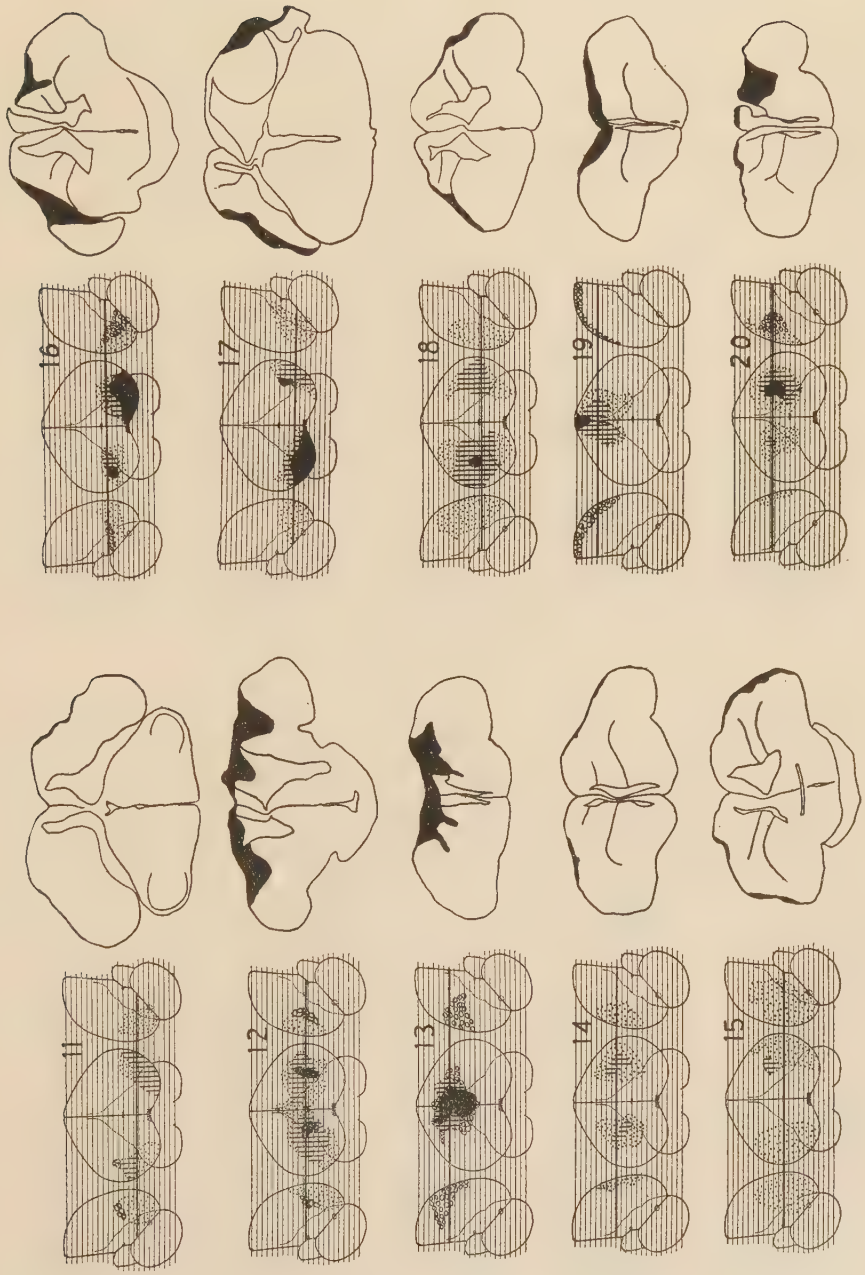

PLATE II

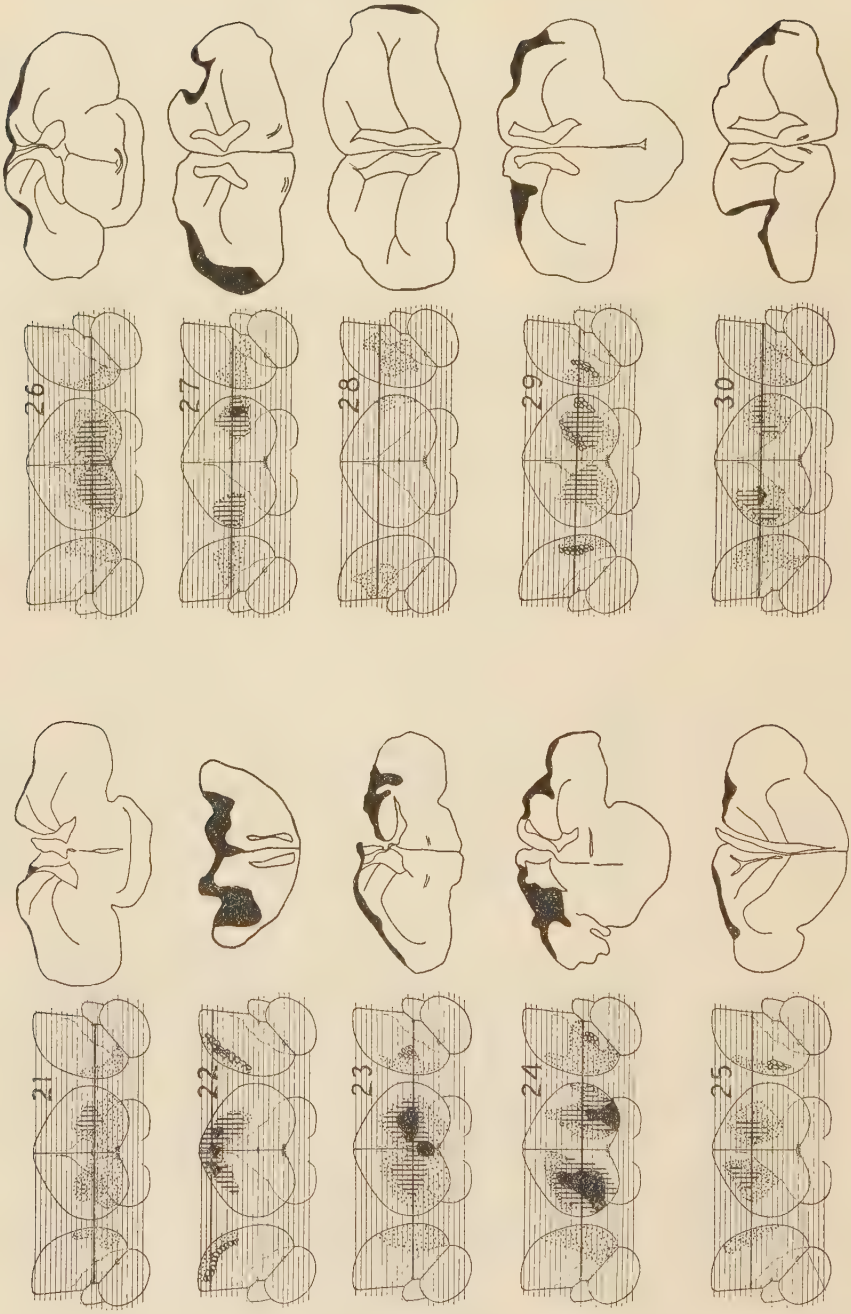

PLATE III

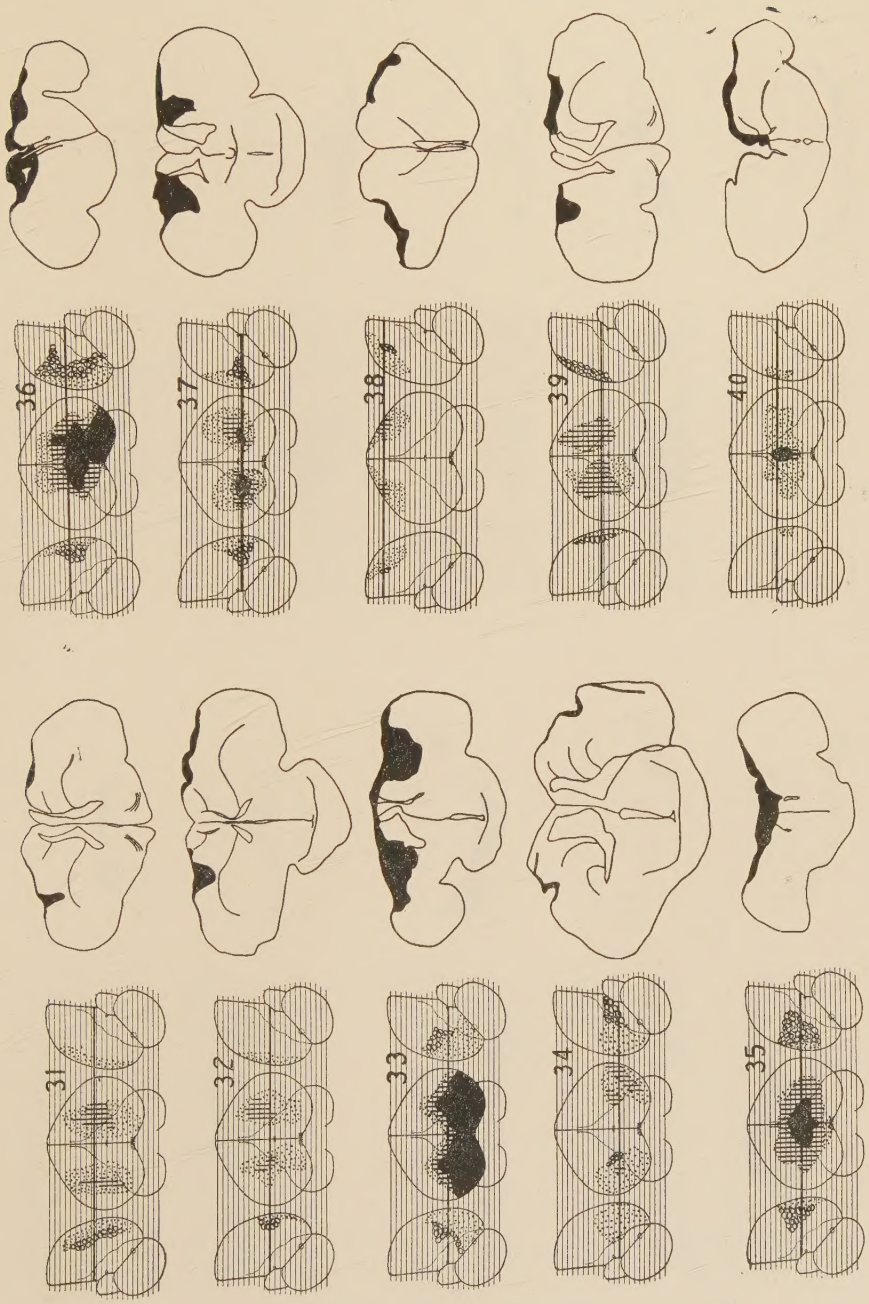

PLATE IV

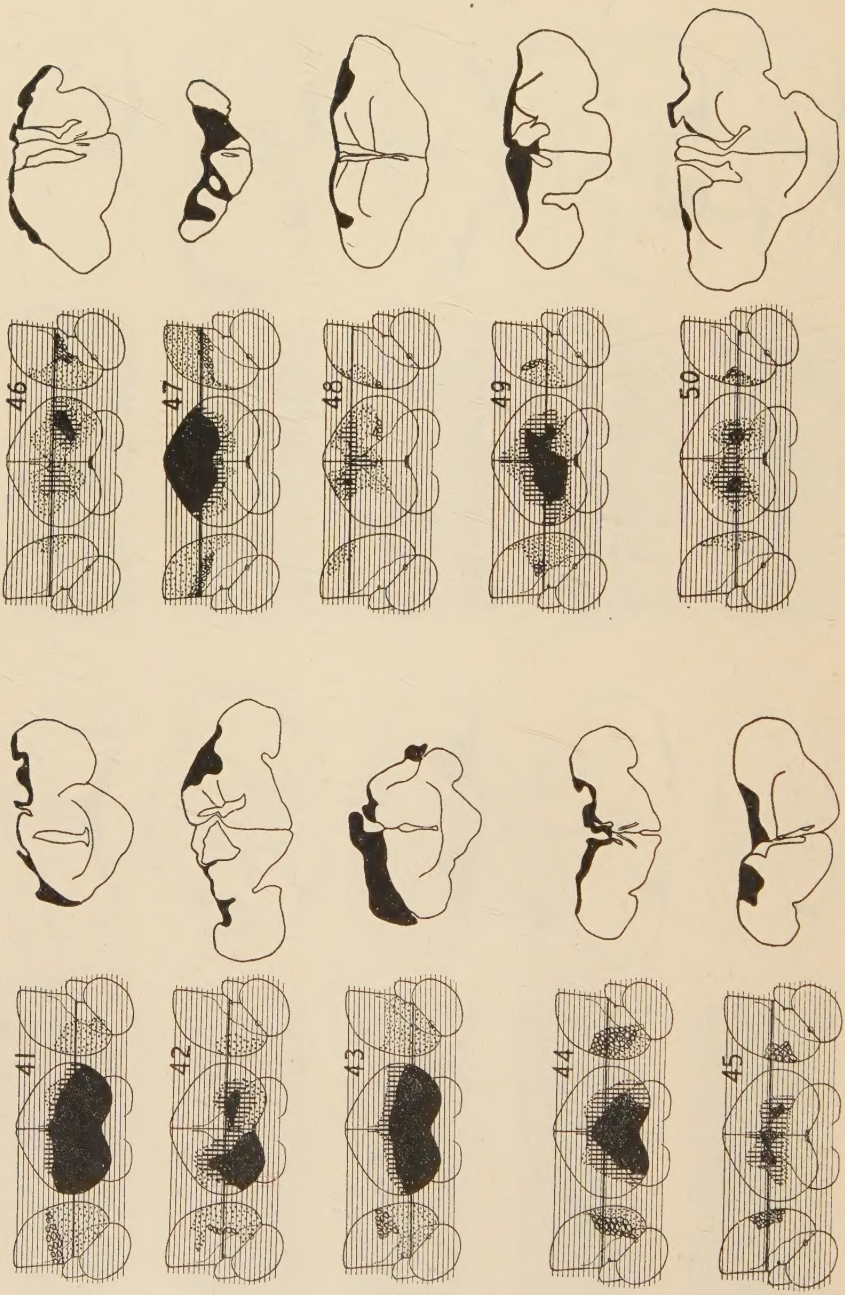

PLATE V